



THE NERC MARINE CENTRES' STRATEGIC RESEARCH PROGRAMME 2007-2012

Theme 4: Biodiversity and Ecosystem Functioning

The natural variety of marine animals, plants and microbes plays an important role in delivering ecosystem functions and benefits. To ameliorate impacts and ensure sustainability in a changing world, we need to be able to detect biodiversity changes as they occur – and predict their likely consequences. This Theme will use a range of approaches, including molecular methods, mesocosms and modelling, to address gaps in our knowledge of how biodiversity affects marine pathways and processes.

Theme 4 comprises three Research Units and seven Work Packages:

Mechanisms regulating marine biological diversity (Plymouth Marine Laboratory)

PML Theme Leader: Paul Somerfield

- WP 4.1 Determining the characteristic scales of variation in biodiversity in coastal and shelf seas
- WP 4.2 Linking benthic dynamics to pelagic ecosystem functioning in shallow seas
- WP 4.3 The influence of biodiversity on ecosystem functioning at different levels of organisation

Resilience and predictability of ecosystem services (Scottish Association for Marine Science).

SAMS Theme Leader: Michael Burrows

- WP 4.4 Contrasting roles of predators and prey in energy flows
- WP 4.5 Microbial mediation of primary productivity and algal biodiversity
- WP 4.6 Linking habitat complexity, size diversity, and invasion-related changes in species diversity to the delivery of ecosystem services

Recruitment and survival in coastal ecosystems (Marine Biological Association)

MBA Theme Leader: Colin Brownlee

- WP 4.7 Functional responses of intertidal assemblages to environmental change

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Theme 4: Biodiversity and Ecosystem functioning

Strategic setting

The global economy has a heavy reliance on the goods and services provided ‘for free’ by the ocean and coastal waters. Whilst we are familiar with the direct benefits of commercial (and recreational) fisheries in providing food from the sea, the indirect and aesthetic worth of maintaining a diverse range of other marine organisms is not easy to assess. Nevertheless, those calculations have been made, giving estimates of a worldwide total value for marine services of \$21 trillion per year (Costanza *et al* 1997) and ~£40 bn per year in the UK (IACMST, 2002). Many of those services and processes, such as the breakdown of organic waste from human populations or the supply of oxygen, go unnoticed until ecosystems collapse.

The next 20 years are expected to involve unprecedented changes in both the physical environment and human demands on the sea, nationally and globally. The UK government is committed to evidence-based, sustainable management of its territorial waters, for the social and economic benefit of society – with the overall goal of achieving “clean, safe, healthy, productive and biologically diverse oceans and seas” (Defra, 2002, 2005a). The development of a more holistic, ecosystem-based approach has particular urgency in the context of fishery management, not only at the national level (PMSU, 2004; RSE, 2004; RCEP, 2004; Defra 2005b), but also at European (CFP, 1998) and global scales (FAO, 2003; Turrell, 2004). Integrated management of coastal habitats and species is also a priority for UK countryside and conservation agencies (EN/NE, SNH, CCW and JNCC); for bodies tasked with maintaining environmental quality standards (EA, SEPA); and for regional coastal zone managers. Such an approach is expected to provide a unifying principle for the UK Marine Bill (currently being drafted by Defra), and already features strongly in a raft of marine-related European strategies, policy frameworks and planning initiatives (including the emerging European Marine Strategy, the EC Habitats Directive, the EC Water Framework Directive, the EU Sustainable Development Strategy, the proposed Marine Framework Directive, and the European Platform for Biodiversity Research Strategy Action Plan).

These policy actions and aspirations are to be welcomed. Unfortunately there remains a major knowledge shortfall, that will make their implementation difficult. Marine ecosystems are large (without clear-cut boundaries), fluid, and difficult to access. Furthermore, many of their key biotic elements are microscopic. It is therefore not surprising that we have imperfect – and inadequate – understanding of how their functioning depends on biodiversity and productivity, and how these relationships will respond to climatic and anthropogenic change. Are some marine species more important than others? Which should be included in monitoring programmes as indices of ‘ecosystem health’? How applicable, if at all, are conservation theories and strategies developed for terrestrial or freshwater habitats? Indeed, are marine ecosystems ‘manageable’ in the conventional sense, or is the issue essentially one of damage limitation? Many other uncertainties surround the fundamental processes regulating marine biodiversity, and the role that biodiversity plays in the sustained delivery of marine ecosystem goods and services.

As indicated above, a panoply of national and international bodies share responsibility for the stewardship of shelf seas and coastal waters, regulating the diverse human uses of these environments. To apply the ecosystems approach for both exploitation management and conservation (e.g. through marine protected areas), they not only require new understanding but also new, soundly-based and cost-effective methods to evaluate the status of marine biodiversity and its functional role. This Theme cannot meet all their needs, but it will (together with Theme 6, and other parts of Oceans 2025) make a significant contribution to the scientific underpinning of marine resource management, primarily through better models of the delivery of marine ecosystem services, focussing on marine ecosystem-diversity interactions that are currently poorly understood.

Existing process-based marine ecosystem models, such as ERSEM (Blackford, 1997), have proved useful in delivering first-order approximations of the ecosystem services provided by functional groups of organisms. However, by covering a broad range of interacting physical, chemical and

biological elements of the ecosystem, such models have necessarily sacrificed detail at the species level and thus the importance of species diversity. Species and their interactions are included in food web models, usually adopting a trophic mass-balance approach (e.g. ECOPATH/ECOSIM, Christensen & Pauly, 1992). Such models give good predictions of equilibrium biomass of dominant species but are highly selective about the species interactions included, usually higher predators, with other trophic groups lumped together or ignored. Both types of models lack realistic ecological processes, such as population dynamics and density-dependent regulation of population sizes. There is a clear need for integration of greater realism into such models for better management of marine bioresources in an ecosystem context (Barange, 2005).

In addition to the Convention on Biological Diversity (CBD) and the European policy frameworks and directives referred to above, the international framework for research relating marine biodiversity to ecosystem benefits is provided by GLOBEC (under IGBP, SCOR and IOC) and DIVERSITAS (established by ICSU, IUBS, SCOPE and Unesco). Until recently, DIVERSITAS was almost exclusively terrestrial; however, a marine cross-cutting component is now being developed, with strong UK involvement (including researchers involved in Theme 4). This is expected to significantly increase opportunities for international collaborations and inter-comparisons during the lifetime of Oceans 2025.

Theme-wide science aims

The overall aims of Theme 4 closely match the high-level research priorities identified in NERC's current strategy 'Science for a Sustainable Future, 2002-2007' (NERC, 2002). That document identified the need to improve knowledge on the role of biodiversity in ecosystem functioning, and the consequences of biodiversity loss on ecosystem processes. Theme 4 also matches six out of seven of the priority topic areas provisionally identified in NERC's new strategy, due in 2007 (www.nerc.ac.uk/consult/strategy07/). In the marine context, the following goals are challenging yet timely:

- To identify the critical species-level processes needed for next-generation ecosystem models that will effectively characterise the effect of marine biodiversity on ecosystem functioning. This may either involve extending and refining existing approaches, or developing entirely new ones.
- To understand how resilient and predictable marine ecosystems are in response to environmental change, including habitat modification, species loss and species invasions, in realistic physical environments.
- To determine the role of trophic interactions in controlling energy flow, and in contributing to the diversity and structure of marine ecosystems and their response to change.
- To identify the important temporal and spatial scales of variation in coastal marine biodiversity.
- To describe links between biodiversity and ecosystem function at different levels of biological organisation and complexity.

In addition to the above, Theme 4 will address more specific knowledge gaps, with emphasis on:

- The extent and importance of microbial diversity in coastal systems.
- The extent to which knowledge of benthic dynamics is essential for understanding pelagic ecosystem functioning in shallow seas; in particular, how the reproductive output of benthic invertebrates contributes seasonally to pelagic systems.
- The importance of viral and fungal pathogens as well as the diversity of bacterial-algal interactions in controlling ecosystem functioning at key trophic levels
- The role of biotic and abiotic factors in determining recruitment success for key intertidal species (fucoid algae).

We will use experimental and modelling approaches to determine the effects of human-driven changes in diversity, and the potential consequences for the functioning of ecosystems. Our focus in this Theme is on coasts and shallow seas, since that is where interactions between human

populations and the marine environment are most intense, and where new knowledge is critically needed to maintain ecosystem services to society through the coming decades and centuries. Coastal and nearshore ecosystems are tractable for experimental and modelling studies, and benefit from many extensive longterm datasets, including the Sustained Observations (SOs) to be maintained in Theme 10.

Centres' contributions

Theme 4 comprises three Research Units (delivered by PML, SAMS and MBA.) and seven Work Packages. The PML work will focus on quantifying variability in coastal seas; the links between benthic and pelagic systems; and the relationships between diversity and function at different levels of biological organisation. SAMS will undertake complementary studies of the relationships between biodiversity and ecosystem services and will also investigate the role of trophic interactions in the resilience and stability of coastal ecosystems. The MBA contribution (of shorter duration) focuses on recruitment processes in coastal ecosystems, integrating molecular and cellular studies of early life history stages in biofilms with population and community processes closely linked to the work at SAMS, and complementing that at PML.

Productive working links already exist between these three Centres, developed through joint contract research, responsive mode grants and EU programmes (e.g. the EU network of excellence Marine Biodiversity & Ecosystem Functioning, MarBEF). Such collaboration and coordination will be strengthened in Theme 4; together, the proposed research will significantly enhance our understanding of the role of marine biodiversity in ecosystem functioning for UK coasts and shelf seas.

Mechanisms regulating marine biological diversity

Contribution to Theme 4 by Plymouth Marine Laboratory

Background

Using integrated multidisciplinary field and laboratory studies we will investigate the factors and mechanisms controlling plankton and benthos biodiversity at short and long time scales. Temporal changes revealed by long-term studies of marine ecosystems are particularly important because of growing concerns about climate change. Changes in the marine food-web may have profound consequences for ecosystem dynamics, and hence the provision of marine living resources (Beaugrand *et al* 2003, Ware *et al* 2005, Platt *et al* 2003). New approaches, particularly molecular techniques, reveal the enormous diversity, particularly of microbes, involved in the pelagic food-web. This diversity is important for biogeochemical processes (Arrigo, 2005), trophodynamic interactions and ecosystem dynamics (Irigoien *et al* 2004), and both natural and anthropogenically-induced ecological change (Beaugrand *et al* 2002). Microbial biodiversity is poorly described, yet it is a key factor in controlling the functioning of the Earth system. This research will make an important contribution to NERC priorities in describing biodiversity, and to international initiatives such as DIVERSITAS, IMBER and the International Census of Marine Life. As such, it strengthens the science-policy interface that integrates biodiversity science for human well-being.

Overall scientific aims and approach

We aim to utilise the extensive time-series from the Western Channel Observatory (WCO, SO 10) and to do experimental studies at the same site. This has been the basis of previous pelagic biodiversity and ecosystem functioning research (PML station L4; Irigoien *et al* 2002, 2004). Molecular methods will be developed to track microbial diversity and production, meroplankton, and predator-prey interactions. We will also sample at a number of linked sites, to improve our ability to predict, detect and understand changes in the functioning of biodiversity within coastal ecosystems. Within marine science, approaches have tended to be sectoral; for example, with pelagic, benthic and microbial ecology being regarded as relatively separate disciplines. We aim to integrate these disciplines with an emphasis on synergies between them, and a focus on important biodiversity-related processes in shelf seas and coastal waters which are absent from, or poorly

represented in, current ecosystem models. In particular, we aim to determine the importance of factors associated with seasonal cycles in pelagic communities, and the significance of benthic-pelagic coupling in shallow-water environments, to the overall functioning of the coastal ecosystem. This knowledge will be used to examine how coastal ecosystems may alter in response to long-term drivers such as climate change, acidification and eutrophication.

WP 4.1 (PML) Determining the characteristic scales of variation in biodiversity in coastal and shelf seas

Specific objectives

- i) Develop molecular methods to quantify microbial biodiversity and functioning
- ii) Identify changes in coastal ecosystem biodiversity and function using long-term data from SO 10 (Western Channel Observatory, PML station L4)
- iii) Determine the characteristic scales of spatio-temporal variability in coastal and shelf seas.

Rationale and approach

A large array of measurements have been collected regularly from the long-term observatory site at L4 (designated SO 10 in Oceans 2025) and these data have provided new understanding of the role of zooplankton and phytoplankton diversity in the functioning of the Western English Channel (Pond *et al* 1996; Rodriguez *et al* 2000; Irigoien & Harris, 2003). Whilst maintaining these studies, we intend to include important microbial components that have not yet been studied at the same intensity.. Metagenomic libraries are an increasingly valuable tool for discovering novel biochemical pathways and linking them to distinct microbial taxa (Béjà *et al* 2000; Venter *et al* 2004). Using large-insert clone libraries (e.g. Bacterial Artificial Chromosomes (BACs) and Fosmids) constructed at PML we will identify microbial taxa and link their function to their phylogeny. We will construct and deploy microarrays to track microbial diversity and functionality through time at SO 10 and associated sites. We have archived (at -80°C) weekly samples for the last 6 years that will provide the DNA to develop a long time-series of changes in microbial functional diversity that we can relate to the large body of environmental data for SO 10, and therefore test emerging ideas about microbial functional diversity.

Some groups of heterotrophic bacteria form large globally distributed populations (Giovannoni & Rappé 2000, Morris *et al* 2002) while others only occur in large numbers in particular environments or at certain times (Rappé *et al* 2000), suggesting differences in ecological strategies (r versus K, specialists versus generalists). To understand functional redundancy among heterotrophic bacteria it is important to distinguish between processes driven by single versatile groups and those driven by many populations of different groups, and to be able to study microbial assemblage structure in the field. Bacterial production is generally measured using uptake of radiolabelled compounds, but many prokaryotes utilise complex natural substrates (Del Giorgio & Cole 1998) of unknown composition. We will develop methods to investigate relationships between bacterioplankton community composition and activity (growth rate, production) in their natural environment which do not depend on uptake measurements. While many models designed to explain biodiversity distributions incorporate species interactions, recent work applying neutral models (Hubbell, 2001) have been very successful in explaining the distribution of diversity in terrestrial systems and mechanisms maintaining it (Volkov *et al* 2003, 2005). The presence of microbes with different ecological strategies may buffer the effects of long-term change on ecosystem functioning, and the relative abundance of different taxa identified at a single time or place may reflect dynamic processes operating on all taxa rather than intrinsic differences in ecology between taxa.

The availability of long-term datasets allows the correlation of changes in assemblages with environmental change (Beaugrand *et al* 2002; Irigoien *et al* 2004; Edwards & Richardson, 2004; Warwick *et al* 2002), and the identification of the nature of changes within assemblages over time. Using a wide range of long-term data, including the WCO series, we will identify changes in phenology and interrelationships between species such as predator-prey dynamics and competition.

The vast majority of studies of the impacts of natural or anthropogenic pressures relate to short time and small spatial scales. By combining data from numerous studies (the eco-informatics approach) the effects of pressures on biodiversity operating at medium to large spatial scales, and medium to long spatial scales, can be examined. Since these are the spatio-temporal scales at which management may be applied, and the effects of policy decisions are manifest, changes at these scales need to be understood and monitored.

Methodology

Using a range of molecular techniques (e.g. microarrays, stable-isotope probing [SIP] and metagenomic libraries) we will develop and deploy tools to map fluctuations in microbial (viruses, pelagic and benthic bacteria and archaea) diversity and functionality. DNA will be extracted from samples collected in a carefully designed field programme focusing on, but not confined to, SO 10 and selected benthic stations in the Western Channel. Large-insert vectors will be used to construct metagenomic libraries which will be screened by PCR, FISH etc. to identify clones containing genetic markers and functional genes. Data from these inserts will be used to construct microarrays to map changes in microbial diversity and abundance, which will be deployed in the field programme. We will combine flow cytometry, cell sorting (Sekar *et al* 2004), dual staining and chemical labelling to study turnover rates of important marine heterotrophic prokaryotes (e.g. *Pelagibacter ubique* and SAR86) in the natural environment and relate these to their known nutrient and energy usage. We will measure the cell-size of taxa using a combination of flow cytometry (Robertson *et al.* 1998) with cell sorting, differential size filtration and microscopy. Carbon conversion factors (Loferer-Krößbacher *et al* 1998; Posch *et al* 2001) will be used to determine biomass and production of different groups. The resulting method will be deployed to determine natural variability in prokaryotic production. We will develop a model system to determine the extent to which microbial assemblages exhibit neutral properties and use it, with the molecular results, to examine the consequences of different global change (pH, temperature) scenarios.

We will collect, collate and combine data from widespread studies, including SO 10. Among our primary sources will be information held by the NMBL. We will develop methods for analysing changes in taxonomic (Ellingsen *et al* 2005, Leonard *et al* 2006) and functional (Petchey & Gaston, 2002) community structure by univariate and multivariate methods and use them to identify patterns of species interrelationships (particularly using the SO 10 data series) and to determine the relative effects of anthropogenic pressures and environmental changes over a range of spatial and temporal scales. We will determine the statistical power (Sommerfield *et al* 2002) of various long-term (Warwick *et al* 2002) or spatially widespread (e.g. Ellingsen *et al* 2005) programmes to detect specific changes in assemblage structure, with a view to providing guidance on the appropriate methods for detecting the effects of long-term environmental change against a background of natural, but changing, environmental variability.

Summary WP 4.1 research plan and deliverables

2007 - 09	<ul style="list-style-type: none"> Develop methods for tracking microbial diversity and function through time using microarrays and deploy them at SO 10 (L4) Develop and deploy methods for <i>in situ</i> study of turnover rates of specific groups of marine prokaryotes
2007 - 10	<ul style="list-style-type: none"> Determine how biological assemblages change in response to changes in key environmental pressures/drivers over a range of spatial and temporal scales
2007 - 12	<ul style="list-style-type: none"> Analyse data from SO 10 to elucidate patterns and the processes driving change Determine the spatio-temporal variability in assemblage structure in pelagic and benthic systems under unimpacted (or null hypothesis) conditions and the relative impacts of different pressures.

WP 4.2 (PML) Linking benthic dynamics to pelagic ecosystem functioning in shallow seas

Specific objectives

- i) To quantify the proportion of benthic production exported to coastal pelagic systems as biomass

- ii) To quantify the role of benthic larvae in coastal pelagic systems
- iii) To develop molecular methods for routine identification of benthic larvae
- iv) To develop a molecular approach to determine prey selection in zooplankton
- v) To resolve links between prey diversity, feeding choices and reproductive success in holo- and meroplanktonic species
- vi) To estimate the effects of a range of global changes (temperature, pH, UV) on zooplankton dynamics and production.

Rationale and approach

In temperate seas a substantial amount of energy and biomass is transferred from the seafloor to the water column in the form of reproductive products and larvae. Eggs develop into larvae, many of which are planktotrophic. These temporary plankton, termed meroplankton, may live in the plankton for several weeks, competing with holoplanktonic (permanent plankton) grazers, and themselves being preyed upon by planktonic predators. Events in the plankton can determine the number of recruits returning to the seafloor. Difficulties in identifying larval invertebrates in the plankton, and associating them with their parent populations, have hindered the quantification of their role in key ecosystem processes. We will address this using molecular techniques, samples from SO 10, and a targeted benthic sampling programme at and around the SO 10 stations. We will quantify the proportion of benthic production exported from the benthos to the plankton in different habitat types and partition the export between different species. We aim to identify the species making the most significant contribution to the meroplankton and the annual pattern and timing of larval release in the dominant species. We will compare our results with historical estimates, for which among our primary sources will be information held by the NMBL.

We will determine the impacts of changes in prey diversity on the pelagic foodweb and assess the potential for competitive and predatory interactions between mero- and holoplankton. *Calanus helgolandicus*, a holoplanktonic copepod, is an important component of pelagic marine ecosystems, grazing microplankton and ciliates and being preyed upon by fish larvae, juveniles and adults of commercially important fish (Bonnet *et al* 2005). Molecular (PCR-based) methods have recently been used on marine organisms (e.g. Symondson 2002, Vestheim *et al* 2005, Blankenship & Yavanos, 2005), to demonstrate that DNA from consumed prey is not completely degraded during digestion. We propose to develop a PCR-based method and use it to investigate feeding preferences of mesozooplankton such as *C. helgolandicus* and dominant meroplankton species. For *Calanus* there are strong interactions between diet, reproduction, development and recruitment. There is an ongoing debate about the relationship between diet (particularly diatoms: Paffenhöfer *et al* 2005) and embryonic development (Irigoiien *et al* 2002; Ianora *et al* 2004; Jones & Flynn, 2005). We will explore the hypothesis that compounds in diet affect the expression of *Calanus* Hox and ParaHox developmental regulators epigenetically, thereby providing a link between maternal nutrition and offspring viability. Measuring food quality is difficult, but it is crucial for understanding zooplankton trophodynamics (Stoecker & Capuzzo, 1990; Ederington *et al* 1995, Pond *et al* 1996). Little is known about the nature and identity of key compounds in potential prey. We will identify and isolate potential key organic compounds from prey, and use them to test their influence on mesozooplankton grazing choices (Cary *et al* 1992).

Methodology

We will investigate a range of genes (e.g. 16S/18S, cytochrome oxidase I,) for use as systematic markers for the discrimination of meroplanktonic species, and undertake a large sequencing effort of benthic adults to increase the library of available sequences. Following detailed descriptions of their morphology we will sequence a target gene from meroplanktonic organisms and compare sequences with the library from adults to confirm their identity. We will refine molecular libraries to allow identification of dominant meroplanktonic larvae at SO 10 throughout the year by probing samples or by amplification and RFLP. We will collect benthic samples regularly through the year at benthic sites selected to represent different habitat types and quantify production by cohort analysis. We will quantify interannual variability in the quantity and timing of reproductive output

of significant species using histology, image analysis and flow cytometry, and investigate potential factors driving it. Molecular probes will be used to identify newly settled juveniles.

We will obtain 18S rDNA sequences from potential prey of *C. helgolandicus* and other meso-zooplankton at SO10 by interrogating sequence databases, and amplify (using universal primers), clone and sequence 18S rDNA from cultured potential prey organisms not in the databases. Oligonucleotide PCR primers will be designed to amplify and discriminate 18S rDNA of prey species from whole zooplankton and faecal pellets. Feeding experiments on single prey types will determine how long after feeding PCR amplification can detect ingested material. The PCR-based approach will be deployed to assess the prey ingested by *C. helgolandicus* and dominant meroplankton at SO 10 and to relate prey ingested to variability in prey availability.

Using *Calanus* reared on a range of diets and mixtures in the laboratory, quantitative expression profiles will be established for two *Calanus* Hox genes and two ParaHox genes known to be important during *Calanus* development (Lindeque & Smerdon 2003), covering all *Calanus* developmental stages from egg to adult. We will develop a method for introducing dsRNA into *Calanus* adult guts and/or embryos, and use RNA interference to knock out each of the genes to determine the consequences for *Calanus* development. Experimental results will be used to interpret quantitative expression profiles of the four genes from eggs laid in the laboratory by *Calanus* taken from SO 10 over the course of a spring bloom.

Targeted biochemical compounds will be encapsulated in droplets, allowing concentrations and droplet sizes to be selected. Phytoplankton cultures will be enriched with selected nutrients (e.g. phosphorus, nitrogen). Providing these as food, we will conduct grazing, development and egg-production experiments using zooplankton collected at SO 10 and laboratory cultures of phytoplankton and microzooplankton. Experimental results will be used to quantify relationships between food availability, diet, population dynamics and secondary production of zooplankton. Experiments will be extended to measure the effects of variation in environmental conditions (e.g. temperature, pH, UV) on key zooplanktonic processes (e.g. development, reproduction, grazing and predation).

Summary WP 4.2 research plan and deliverables

2007 - 09	<ul style="list-style-type: none"> Identify the timing and annual pattern of larval release in the dominant species Develop molecular methods for the routine identification of larvae of a range of species Develop a PCR-based method to assess prey ingested by mesozooplankton, and deploy it at SO 10
2009 - 12	<ul style="list-style-type: none"> Quantify intra- and inter-annual variability in the proportion of energy and carbon produced in the benthos and exported to the plankton Quantify the impact of meroplankton in the pelagic foodweb
2010 -12	<ul style="list-style-type: none"> Determine the effects of dietary changes on expression of selected <i>Calanus</i> development genes Define the biochemical controls of ingestion, growth and reproduction in zooplankton Quantify relationships between diet and variability in population dynamics and secondary production

WP 4.3 (PML) The influence of biodiversity on ecosystem function at different levels of organisation

Specific objectives

- i) Determine how changes in genetic diversity allow marine viruses to adapt and function
- ii) Clarify how cell-signalling links microbial biodiversity and functioning in marine systems
- iii) Establish the link between diversity in particular genes and tolerance of anthropogenic and natural stress in marine invertebrates
- iv) Experimentally assess the potential effects of changes in the benthos on coastal pelagic systems

Rationale and approach

While there has been considerable effort to investigate how changes in the diversity of large (and relatively easily studied) organisms may alter ecosystem functioning, we know that much smaller-scale processes are also important. Specifically, we will study how changes in the genetic diversity

of viruses determine their ability to function; how bacteria communicate by quorum sensing in natural biofilms to deliver functions which isolated bacteria cannot; how differences in stress tolerance among marine organisms may be determined by their genetic diversity; and how changes in one part of the ecosystem may impact on another. The focus throughout is on biodiversity-related variation which has the potential to drive non-linearities in ecosystem functioning.

Marine viruses are the most abundant particles in the sea, and subject to great selection pressure. The evolution of viruses plays a role in driving the evolution of host populations. Whereas other organisms typically acclimatise to changes in the environment through changes in their metabolism, viruses have no metabolism of their own. For a virus to have a competitive advantage over closely related viruses its genome must evolve, either by adapting genes already present, or by acquiring new ones (Lindell *et al* 2005, Allen *et al* 2006).

Through the production of small, mostly diffusible, signalling molecules bacteria are able to communicate (so-called quorum sensing), monitor their own population density, and regulate expression of multiple genes in a manner analogous to a multicellular organism (Swift *et al* 2001, Withers *et al* 2001). Most studies have examined gene expression in single-species cultures but marine microbes normally occur in mixed populations of prokaryotes and eukaryotes – and some eukaryotes can recognise, and respond to, prokaryotic signalling molecules (Joint *et al* 2002, Tait *et al* 2005). Quorum sensing is important in the development, maintenance and functioning of microbial communities in all marine habitats. We will focus on hard substrates as understanding biofilm development is of commercial importance (biofouling is a multi-billion dollar problem). This is a tractable system to experiment on, and to investigate interactions between bacteria and higher organisms.

At a very high taxonomic level, some groups of marine invertebrates are known to be more sensitive to anthropogenic pressures such as pollution than others (e.g. echinoderms v annelids); furthermore, species characteristic of fluctuating environments (e.g. estuaries) tend to be more tolerant of anthropogenic stress. What is not known is the physiological mechanism. Recent work has highlighted the role of highly conserved molecular pathways orchestrating cellular integrity and homeostasis in response to stress (Gross 2004, Kulz 2005). Differences in the ability of organisms to up-regulate these pathways may determine their ability to respond to natural variation, and therefore pre-adapt them to deal with anthropogenic stress (Moore *et al*, in press). Thus it may be possible to determine the potential responses of organisms to environmental change from knowledge of a small part of their genome.

Using current versions of the ERSEM model, scenario modelling of reduced abundances of benthic organisms (simulating the effects of benthic trawling) in non-stratified waters indicates a greater importance of benthic suspension feeders than would be intuitively expected and cascading effects in the pelagic ecosystem (Allen *et al*, submitted). We will investigate whether empirical data shows the same importance of benthic communities in controlling wider marine ecosystem functioning. Such information will be used in ecosystem model development (Theme 9).

Methodology

Coccolithovirus is a recently discovered group of viruses that infect the globally important marine calcifying microalga *Emiliana huxleyi* (Wilson *et al* 2005). By exploiting informatics we will examine how marine viruses, especially those in the coccolithovirus family, acquire novel genes and adapt existing genes, and how this allows them to remain competitive. We will explore the application of novel approaches (e.g. Clarke & Gorley, 2006) to the multivariate analysis of bioinformatics data in the process.

Molecular techniques (PCR, DGGE, FISH) will be used to track the colonisation of surfaces immersed in seawater to investigate the establishment and development of microbial biofilms. A selection of biofilm-producing bacteria will be genetically modified to produce signal-deficient (knock-out) mutants which will be used in mixed-species experiments to assess the role of chemical communication in the development of microbial biofilms. We will investigate how microbially-

derived signalling molecules in the environment influence the behaviour of selected eukaryotic taxa (e.g. macroalgae), to determine the ecological consequences (links with MBA and SAMS)..

Regulatory regions (e.g. promoter, 3' untranslated regions) will be identified in key genes associated with stress responses (e.g. glutathione-s-transferase) in a range of marine invertebrates from genomic databases. Regions of polymorphism will be identified as far as possible using known sequence information. Promoter regions will be identified using gene-walking techniques and primers designed to enable screening of organisms. We will determine variability in the ability of organisms to up-regulate stress-related cellular pathways in invertebrate groups selected on the basis of their known stress tolerance or ability to live in fluctuating environments.

We will carry out grazing experiments in mesocosms to determine whether soft-sediment benthic assemblages with differing functional-group diversity are capable of substantially modifying and impacting overlying pelagic production in coastal waters through direct suspension-feeding predation. Empirical results will be compared with ecosystem model results to examine the mechanisms involved in benthic feedbacks to the pelagic community and to validate the models.

Summary WP 4.3 research plan and deliverables

2007 - 09	<ul style="list-style-type: none"> Characterise the novel genes acquired by <i>Coccolithovirus</i> and determine the physiological and ecological consequences
2007 - 10	<ul style="list-style-type: none"> Establish the role of bacterially-derived signalling molecules in the development and maintenance of marine microbial and algal communities
2009 - 12	<ul style="list-style-type: none"> Relate polymorphisms in promoter and 3' untranslated regions in key stress-related genes to tolerances to anthropogenic and natural stresses in marine invertebrates Develop a system to expose plankton communities to predation within the mesocosm

Resilience and predictability of ecosystem services

Contribution to Theme 4 by the Scottish Association for Marine Science

Background

Our current understanding of the role of biodiversity in ecosystem behaviour leaves us ill-prepared to manage and mitigate the effects of coming change. Whilst the first steps have been taken in developing an understanding of how physical and biological changes in ocean dynamics might alter species abundances and distributions (Beaugrand *et al*, 2002; Perry *et al* 2005), the consequences of these changes for ecosystem structure and function remain unclear. Consideration of ecosystems as food webs of metabolically-constrained organisms may offer a viable solution (Dunne *et al* 2005; Brown *et al* 2004). All food webs, and therefore all ecosystems, are economies trading in energy, so identifying and understanding the rules governing energy acquisition and transfer (primary production and the timing, direction and strength of trophic interactions) are fundamental to our understanding of ecosystem stability and resilience (McCann 2000; Woodward *et al* 2005).

Stability and resilience in turn underpin the long-term sustainability and predictability of ecosystem services. Existing food-web theory derived from terrestrial and freshwater systems suggests that systems dominated by bottom-up controls, where consumer species have little or no effect on the abundance of their food resources, are inherently more stable than those under top-down predator control (DeAngelis 1975; Schoener 1989). Moreover, if interactions among species are mainly strong, increasing species diversity tends to have a destabilising effect on the ecosystem (May 1973), whereas the converse is true if species interactions are predominantly weak (Berlow 1999). Metabolic theory makes predictions that emphasise body size in addition to taxonomic identity as a critical component of trophic position and consequently ecosystem stability. These predictions are particularly relevant to many larger benthic species, including commercial species, that have planktonic stages and go through severe ontogenetic shifts in trophic status and habitat utilisation.

Because we urgently need answers, and because of the limited applicability of current marine models at the ecosystem level, in this Research Unit we will adopt the more immediate approach of attempting to understand coastal systems as they are: complex systems of interacting species. In so doing we aim to elucidate principles governing how marine ecosystems are put together in terms of the timing, strength and direction of dominant trophic interactions, as well as what the potential consequences of this for the future provision of ecosystem services in a changing environment. We intend to develop quantitative understanding of these species-specific processes for future incorporation into better models of whole marine ecosystems.

Specific goals are given in Work Packages WP 4.4 – 4.6 below. To ensure maximum efficiency in our work, we propose to conduct most of our studies in intertidal and shallow subtidal habitats, which tend to be well-characterised, accessible and tractable systems. We will make extensive use of the SAMS Loch Linnhe Artificial Reef (SAMS 2005; WP 4.6). This unique medium- to large-scale facility offers the opportunity for controlled ecological experimentation in spatially replicated subtidal rocky habitats. Microbial systems (WP. 4.5) will be investigated in controlled laboratory experiments, making use of the SAMS-hosted CCAP National Facility (NF 3).

WP 4.4 (SAMS) Contrasting roles of predators and prey in energy flows

Aims and rationale

Intertidal and shallow-water habitats offer accessible examples of ecosystems under varying directions of trophic control. Strong top-down control is evident in some elements of rocky shore systems. The limpet grazer-biofilm-macroalgae trophic chain is a good example (Burrows & Hawkins, 1998; Thompson *et al* 2004). By contrast, other unconnected components of rocky shore systems, such as predators (Hughes & Burrows, 1993), barnacles and mussels (Sanford *et al* 1994; Leslie *et al* 2005), are under bottom-up control, as are sandy beach flatfish nursery grounds (van der Veer & Witte, 1993). Taking advantage of the prevalence of these systems around the British coast, we propose a macro-ecological experimental study that will first identify the directionality of forcing in different study systems, and then test predicted responses of top-down and bottom-up structured systems to changes in physical conditions that simulate climate change.

Predators in marine systems have the capacity to exert top-down control on prey populations. However, if environmental change drives prey assemblage flux, the foraging plasticity of the predator becomes a key factor in determining the vulnerability of the ecosystem to that change. This plasticity is not only in terms of the predator diet width but also the rapidity with which predators can adapt their diets. For example, the intertidal dogwhelk *Nucella* consumes both barnacles and mussels, and can prevent mussels from dominating intertidal habitats. However, diet switching may take several years for individual snails allowing mussels recruiting in boom years to gain a foothold in previously barnacle dominated habitats (Hughes & Burrows, 1993). These temporal mismatches between predator diet choice and prey availability are probably most widespread where prey handling requires specific skills. It has been suggested, for example, that temporal specialisation by generalist killer whales may have been responsible for the sequential and dramatic declines in the abundance of multiple marine mammal species in the North Pacific (Springer *et al* 2003). If we are to predict the influence of top-down control in changing marine environments, therefore, we need an appreciation of the capacity of marine predators to flex their foraging patterns and diet choice in the face of environmental change.

Specific objectives

- i) Contrast responses to global change in top-down versus bottom-up structured foodwebs.
- ii) Investigate the capacity for marine generalist predators to exert top-down control on alien prey assemblages given varying levels of prey biodiversity prior to the environmental change.

Approach and methods

With top down control, consumer growth and mortality should be strongly density-dependent since consumers will have a strong effect on their resources, while bottom up control should show no

density dependence of growth and mortality. Directionality of trophic forcing in different study systems can therefore be diagnosed by experimentally manipulating populations of consumer species. For example, on rocky shores, populations of limpet grazers will be manipulated to determine effects on their growth rates, as well as those of the biofilm and macroalgae. Limpet growth should be strongly density dependent since these grazers control food availability in the biofilm (Boaventura *et al* 2003; Thompson *et al* 2004). Manipulation of the biofilm will emulate potential effects of changing climate: increased drying and rock surface temperature, increased rainfall and wind (in liaison with MBA). Manipulation of the densities of filter feeders should produce no density-dependent effects on their growth or mortality since filter feeders are thought to have no effect on the abundance of their food. This will be tested by sampling phytoplankton above cleared and non-cleared mussel beds or barnacle-covered rock. Moreover, manipulation of food supply will be possible by selecting areas of similar wave exposure and phytoplankton abundance but different flow regimes. Since food supply is limiting in such systems, we expect an effect on filter feeder growth and biomass, especially where space is not limited.

In shallow-water flatfish nursery grounds, sites with more fish tend to have more detritus feeders, such as *Arenicola* and *Crangon*. Like the phytoplankton-filter feeder system on rocky shores, sandy beach foodwebs rely primarily on carbon fixed elsewhere (macroalgal and phyto-detritus). This openness may be typical of bottom-up controlled marine systems. Population dynamics in key species of areas with contrasting natural variation in supply of fish larvae will be compared to determine the dominant control direction. System models will be developed to encompass density-dependent regulation of consumers, and the relative roles of food- and space-limitation in filter feeder populations, using agent-based (Grimm *et al* 2005) and matrix approaches (Caswell, 2000).

We will use benthic invertebrates (the sea urchins *Psammechinus miliaris* and *Paracentrotus lividus*), which have a different predilection towards omnivory and which show different foraging responses as a model predators (Otero-Villanueva *et al* 2006). Cultures of urchins will be lab-reared (Kelly *et al* 2000) in divergent foraging regimes, ranging from high- to low-diversity diets to create behaviourally generalist and specialist urchin varieties. The mature urchins will then be exposed to simulated environmental change manifest through novel prey types including invasive alien invaders. The foraging success, and more significantly their abilities to impact prey abundance, will then be investigated. Mature wild urchins from divergent (complex and simple) local habitats (Hughes *et al* 2005) will be similarly challenged and their behavioural plasticity used to explore how established predators with different foraging histories are able to modulate environmentally driven changing prey assemblages.

Summary WP 4.4 research plan and deliverables

2007 - 08	<ul style="list-style-type: none"> Manipulate grazer densities in rocky shore systems to determine the strength of top-down control Rear trophic specialist and trophic generalist urchins
2007 - 11	<ul style="list-style-type: none"> Develop and test models of top-down and bottom-up controlled systems using coupled population models and agent-based approaches
2008 - 09	<ul style="list-style-type: none"> Establish strength of bottom-up control in flatfish nurseries and benthic filter feeder assemblages
2009 - 10	<ul style="list-style-type: none"> Manipulate local conditions to determine the susceptibility of top-down and bottom-up control to environmental change
2009 - 11	<ul style="list-style-type: none"> Experimental testing of foraging success of urchins in contrasting prey assemblages

WP 4.5 (SAMS) Microbial mediation of primary productivity and algal biodiversity

Aims and rationale

The interactions between primary production (by macroalgae, microalgae and photosynthetic bacteria) and decomposers (heterotrophic bacteria and archaea) in the marine ecosystem have profound implications to the amount and flow of carbon and other elements within marine

ecosystems from the micro- to ocean-basin scale (Azam, 1998). The nature, strength and direction of the interactions may vary from negative effects linked to nutrient competition (e.g. Joint *et al* 2002) or cellular attack (Mayali & Azam, 2004), to positive effects such as re-mineralization (Azam *et al* 1983) or the supply of co-factors for growth (Croft *et al* 2006). Whilst bacterial services to primary producers are important, they have been poorly quantified. We predict that the nature of this interaction is likely to depend on the speciation and richness of the heterotrophic bacterial assemblage within an ecosystem. This in turn will act to influence the level of primary production and ultimately the efficiency by which some or all these resources are directed into the wider ecosystem. In this regard, it is generally predicted, and has been demonstrated recently (e.g. Bell *et al* 2005), that increasingly species-rich communities have enhanced ecosystem functioning. The aim of the proposed study is to explore and develop a predictive understanding of the role that prokaryotic diversity plays in influencing eukaryotic productivity.

Microbial contributions to productivity in marine food webs are receiving increasing attention, but the role of microbes as agents of natural selection remains poorly understood. In this context, the greatest volume of information relates to virally-mediated selection pressures on algal and planktonic assemblages (e.g. Müller *et al* 2000), but no comparable data are available for eukaryotic pathogens. Because selection pressures contribute to the determination of local biodiversity, and also because they might change with changing climate, we propose to study the role of algal pathogens in temperate and polar seas. In particular, we will assess the extent to which oomycete, fungal and viral epidemics constitute a pressure on brown algal populations and how the pattern of such epidemics might change in response to future climate scenarios as has been demonstrated for terrestrial ecosystems (Bergot *et al* 2004; Pounds *et al* 2006). The interaction between these microbes and their macroalgal hosts will be examined with a special emphasis on the oomycete *Eurychasma* (frequently occurring in epidemics; Küpper & Müller, 1999) as a case study.

Specific objectives

- i) Quantify the strength and direction bacterial species richness and composition plays in influencing phytoplankton growth and photosynthetic efficiency.
- ii) Identify bacterial community structures (size/composition) that may predict stability and/or resilience or shifts in algal productivity.
- iii) Assess prevalence of eukaryotic pathogens in algal populations – correlate with population recruitment and primary productivity.

Approach and methods

Phycospheric (algal-associated) bacteria comprise a sub-set of typical marine bacterial taxa (Green *et al* 2004), but by their physical proximity to algal cells, can exert potentially important influences on phytoplankton productivity. From our sequenced (16S rDNA) bacterial collection ($n \geq 170$) cultured from dinoflagellates, diatoms and coccolithophores – which include a number of ‘unculturables’ such as SAR86-like organisms – we will assemble random bacterial communities (species richness = 1, 2, 4, 8, 16, 32) that will be added to our ‘axenic’ algal model, *Scrippsiella trochoidea*, a globally-distributed neritic dinoflagellate. Using fast repetition rate fluorometry calibrated to our model alga, we will monitor growth and photosynthetic efficiency at regular intervals over 3-4 weeks of incubation in each replicate. Community assembly and experimental design will essentially follow that described by Bell *et al* (2005). Results will enable us to: i) identify the direction and strength bacterial diversity plays in influencing algal productivity; ii) specifically examine the influence bacteria have biomass production and the efficiency by which inorganic carbon is drawn-down; iii) and develop a predictive understanding of how bacterial diversity may contribute to ecosystem stability or resilience, and act as a predictor of change in ecosystem functioning.

We will also develop real-time PCR-based molecular tools for the detection and quantification of *Eurychasma* and other pathogens in algal populations. In the laboratory, we will investigate the interaction of *Eurychasma* with its host species at the cellular and molecular level. The release of

the first brown algal genome (*Ectocarpus siliculosus*) will provide new opportunities to apply post-genomics tools (proteomics, metabolomics). We will look for cellular markers of pathogen attack and defence. These will be used in molecular ecology/ecophysiology studies, linking pathogen attack to primary productivity and environmental factors such as temperature, salinity and nutrients, and ultimately be applied in algal populations in the field. The results will help us to predict the occurrence of eukaryotic pathogen epidemics, and to understand their function in structuring macroalgal populations and their role in the flux of energy and matter in marine systems.

Summary WP 4.5 research plan and deliverables

2007	<ul style="list-style-type: none"> FRRF calibration of model alga; complete bacterial isolations and 16S rDNA sequencing of diatom-associated bacteria (n ≥ 200 bacteria). Publish bacterial community structure of key diatom species
2007-08	<ul style="list-style-type: none"> Develop real-time PCR assay to identify <i>Eurychasma</i> in the field. Report/publish assay development
2008-09	<ul style="list-style-type: none"> Begin and conclude culture experiments; analyse data; quantify effects and identify community structures important to stability, resilience or impact on algal productivity.
2010	<ul style="list-style-type: none"> Report and publish findings to scientific community and stakeholders
2010-12	<ul style="list-style-type: none"> Field based surveys of <i>Eurychasma</i> infection levels across geographic gradient and seasonally. Integrate infection levels to brown algal species type/distribution and influence on coastal productivity. Report/publish findings to scientific community and stakeholders

WP 4.6 (SAMS) Linking habitat complexity, size diversity and invasion-related changes to the delivery of ecosystem services

Aims and rationale

Biological assemblages, with their associated processes, interactions and size structures, contribute to biogeochemical cycles and ecosystem stability and functioning (Odum, 1971; Loreau *et al.* 2001; Woodward *et al.* 2005), and hence the provision of services such as fisheries. Microcosm studies (Naeem *et al.* 1994) and observations of natural perturbations (Tilman & Downing, 1994) have shown that a reduction in species- and size-diversity, which are closely linked to factors such as habitat complexity (Johnson *et al.* 2003), current exposure (Guichard & Bourget, 1998) and inter-specific competition (Byers, 2000), are highly influential in determining the stability of ecosystems and their susceptibility to biological invasion (Kennedy *et al.* 2002). However, serious gaps remain in our understanding of the linkages between abiotic and biotic factors in the delivery of ecosystem services, particularly as we increasingly modify the coastal zone (e.g. through offshore windfarms and coastal defences), and our coastlines are subject to invasions of non-native species.

Our aim is to test the hypothesis that increasing habitat complexity will increase species- and size-diversity in the marine benthos and to link this to ecosystem services including overall production, the provision of commercially important fishery-species (particularly juveniles) and to determine the extent to which size- and species-diversity increase ecosystem resilience to biological invasions.

Specific objectives

- i) To quantify the role of habitat complexity in determining species- and size-diversity under a range of environmental conditions
- ii) To relate habitat-induced changes in species- and size diversity to system stability and resilience to biological invasions.
- iii) To measure how habitat complexity, and the scale of that complexity, can be modified to suit commercially relevant species under a range of environmental conditions.

Approach and methods

The proposed research will consist of laboratory and field experiments where habitats are manipulated to provide varying degrees of complexity. Field observations will include those on the Loch Linnhe artificial reef that has been created over a well-characterised environmental gradient with varying degrees of complexity. Measured ecosystem functions will comprise biodiversity,

production/respiration and counts of the juveniles of commercially relevant species. Biodiversity (both size and species) will be measured through field observations and photo-analysis. Production/respiration will be measured by either the development of a hand-held underwater oxygen probe or by Winkler titration of water samples taken from isolated field units. Initial work may involve the recovery of test substrata to aquaria for detailed measurements and observations.

In further laboratory-based experiments, communities of sub-tidal benthic organisms, manipulated to provide high and low levels of species diversity, interspecific interaction and number of trophic levels, will be subjected to invasion using a variety of invasive species representing different trophic levels, including the macroalga, *Sargassum muticum* and the amphipod *Caprella mutica*. Ecosystem stability and resilience will be measured pre- and post-invasion under the various predicted temperature and pH scenarios for 2025, 2050 and 2100. Results of the laboratory experiments will be validated in field trials using underwater video cameras to monitor the influence of habitat complexity on the success of invasion in marine coastal systems.

Summary WP 4.6 research plan and deliverables

2007 – 08	<ul style="list-style-type: none"> Establish small-scale experimental substrata (in addition to that provided by the Loch Linnhe artificial reef) of various habitat complexities
2008 – 09	<ul style="list-style-type: none"> Manipulate species diversity, introduce alien species and monitor community response.
2011 – 12	<ul style="list-style-type: none"> Produce high-quality publications, inform society regarding offshore structure design optimisation to maximise fisheries and minimise susceptibility to invasions.

Recruitment and survival in coastal ecosystems

Contribution to Theme 4 by the Marine Biological Association

Background

Of all marine habitats, the intertidal system is likely to change most in the next 20 years as the pace of human activities and development of the coastal zone accelerates (Thompson *et al*, 2002). Productivity in shallow coastal ecosystems is largely driven by microbial and macroalgal assemblages growing rapidly on hard and soft substrates. Processes occurring in biofilms at the substrate surface determine microbial productivity as well as the probability of macroalgal recruitment (Thompson *et al* 2004) and the extent to which shores are net producers and exporters (dominated by macroalgae) or consumers and importers (dominated by filter feeders). We will focus on functional responses of macroalgae to environmental stressors at the molecular and cellular level which have consequences for population and community level processes and hence ecosystem functioning.

Positive feedbacks exist between microbial and macroalgal productivity: a productive epilithic biofilm facilitates macroalgal propagule development; while growth of macroalgae provides amelioration of stressful extremes for microalgae. Early life history events in the benthic biofilm are subject to both deterministic processes (particularly susceptibility to environmental stressors such as extreme events and grazing control) as well as stochastic events such as the patchy and unpredictable arrival of propagules. The outcomes of the interaction of deterministic processes and stochastic events are mediated by both bottom-up forcing (e.g. nutrients, temperature, light) and top-down regulation of population processes (grazing and predation). Recently the role of stress-related modifiers (e.g. physical stress from insolation, higher temperatures) has been highlighted and shown to be as important as top-down and bottom-up processes in regulating productivity (Thompson *et al* 2004). Studies of diversity and the functional attributes of different unicellular and multicellular elements of the boundary layer (bacteria, diatoms, cyanobacteria, macroalgal germlings and sporelings) are in their infancy. To address these issues we will deploy a modern battery of molecular cellular and imaging techniques (including analysis of gene expression, confocal and 2-photon imaging and electrophysiology) that we have developed in this laboratory

(e.g. Corellou *et al* 2001, 2005; Goddard *et al* 2000; Bothwell *et al* 2006). This will be coupled with well designed, tightly controlled and statistically rigorous field experiments on abiotic-biotic interactions linking strongly with work at SAMS.

WP 4.7 (MBA) Functional responses of intertidal assemblages to environmental change

Specific objectives

- i) Identify the major factors underlying recruitment and survival mechanisms of key species at the molecular and cellular level.
- ii) Identify and characterize mechanisms of short and long term adaptations of fucoid embryos to physical changes.
- iii) Improve understanding of the complexity of chemical, physical and biological interactions in biofilms and the consequences for population and community dynamics.

The production of motile spores for dispersal is a fundamental step in the life histories of many green and brown marine macroalgae (e.g. *Ulva*, *Ectocarpus*). The sensory abilities of spores and other distributional macroalgal stages are especially important once they enter the benthic boundary layer, where they encounter new microenvironments with strong physical (e.g. surface structure, surface charge or light), chemical (e.g. nutrient, ionic gradients or antifouling compounds) and biological gradients (e.g. biofilms). In contrast to motile spores the non-motile zygotes of fucoid algae settle in a random but less widely dispersed manner and need to adapt to prevailing environmental conditions to ensure survival and growth. Fucoid zygotes present a tractable system for studying the molecular mechanisms of perception and adaptation to environmental perturbations. Our evidence suggests that early life cycle stages of fucoid algae are particularly vulnerable to abiotic stress (e.g. Goddard *et al* 2000; Nielsen *et al* 2003a,b) and biological interactions (Thompson *et al* 2004) and this holds true for other species (e.g. Lee *et al* 2006). Our preliminary experiments also suggest that different fucoid species show different physiological features that correspond to their niche specialization, and that these differences can be ascribed to specific sets of cellular signalling-response elements. Understanding these mechanisms is essential for predicting how species assemblages will respond to different environmental change scenarios.

Approaches and methodologies

We will apply a combination of genomic, molecular and cellular biophysical approaches to:

- Identify and characterize specific signalling-response elements in tractable brown algal systems (fucoid zygotes and *Ectocarpus* zoospores) (links with PML).
- Identify molecular adaptations that have given rise to different tolerances to abiotic stress by utilizing the substantial transcriptome databases available through participation in the EU Marine Genomics network of excellence.
- Develop high throughput approaches for species identification *in situ* at the embryo, sporeling and germling level.
- Translate these techniques into field experiments to test the relative importance of stress and biotic interactions on survival, particularly probabilities of escape.
- Determine the level of propagule supply and probabilities of transfer between early life history stages under manipulated levels of grazing pressure and stress (links with SAMS).

Summary WP 4.7 research plan and deliverables

2007 - 08	Characterization of the key life stages that are susceptible to biotic stress
2007 - 09	Identification of key signalling genes involved in abiotic stress perceptions and response
2008 - 09	Experimentally verified models of responses to abiotic stress and grazing perturbations

Theme 4 Synthesis and Concluding Material

Oceans 2025 synergies and wider links

The work proposed here will develop our understanding of biotically-mediated processes in the marine environment, how they can be measured, how they vary, how they are likely to be changed in the future, and what the consequences of such changes may be. As such it is closely linked to other parts of Oceans 2025 (Table 1), especially Theme 6. It draws heavily on existing and new data from long-term observations, especially those from SO 10, but it will also involve innovative and new experimental approaches in the laboratory and field.

Table 1. Main links between Theme 4 and other parts of Oceans 2025

Theme 1	Ocean models, global sea level response to climate change
Theme 2	Diversity in relation to biogeochemical cycles
Theme 3	Consequences of climatically driven environmental change
Theme 6	Relationships between biodiversity and provision of ecosystem goods and services
Theme 9	Processes and parameters for new-generation ecosystem models
Theme 10	Expansion and interpretation of long-term observations; use of data (particularly from SO 10) for analyses and model development

The scientists involved in Theme 4 have widespread existing collaborations with many other UK academic, public sector and private sector research groups (Table 2), with university links involving the hosting, supervision and co-supervision of PhD and Masters students, provision of training, and joint research projects. Main international links are given in Table 3.

Table 2. Main existing science collaborations between Theme 4 and other UK research groups not part of Oceans 2025.

Astra-Zeneca	Long-term patterns, monitoring
BAS	Methods for zooplankton mortality estimation; modelling interactions of predators and prey in the Southern Ocean ecosystem
Cefas (Burnham)	Benthic ecology, development of indicators for management, effects of pressures
Cefas (Lowestoft)	Fisheries ecology, ecological effects of fishing, indicators, recruitment and population dynamics of flatfish
Centre for Ecology & Hydrology (CEH)	Marine-terrestrial comparisons, hydrocarbon degradation through bacteria and bioturbation, protist ecology
Defra	Indicators for marine management
Environment Agency	Management indicators, WFD, National Marine Monitoring Programme
FRS Marine Lab, Aberdeen,	<i>Calanus physiology</i> and ecology; benthic effects of fishing
Marine Ecological Surveys Ltd	Modelling effects of aggregate extraction, trait analysis
National Museum Cardiff	Large-scale patterns, taxonomy
NERC Environmental Bioinformatic Centre (NEBC)	Bioinformatic analysis of genomics and microarray data.
Primer-e Ltd	Statistical methods, software development
Natural History Museum	Tsunami impacts on and the subsequent recovery of shallow water biota in Thailand; nematode ecology and genetics, taxonomy
Queens University Belfast	Stochastic matrix model approaches to community dynamics on rocky shores, mapping shallow water habitats
Univ of Aberdeen	Hydrocarbon degradation through bacteria and bioturbation; isolation of differential transcripts related to stress tolerance
Univ of East Anglia	DMS release during zooplankton feeding, socio-economics
Univ of Bristol	Survival and recruitment of macroalgae
Univ of Edinburgh	EST Analysis
Univ of Essex	Algal cell physiology and photosynthetic efficiency related to bacterial symbiosis, biofilm ecology

Univ of Liverpool John Moores	Carotenoid biochemistry
Univ of Liverpool	Microarray design and printing; screening of bacterial isolates for activity; measures of ecosystem functioning, trait analysis
Univ of Newcastle	Design of complex artificial reefs and modelling of physical structures, electron microscopy of fungal infection processes
Univ of Nottingham	Quorum sensing
Univ of Plymouth	Benthic ecology, experimental ecology, ecosystem functioning, nematode genetics, ecology of intertidal biofilms
Univ of Wales, Bangor	Ecological effects of fishing, meta-analysis, foraging of intertidal invertebrates and optimality theory, recruitment and density dependence of sessile invertebrates; sea urchin genetics
Univ of Wales, Swansea	Phytoplankton blooms: A "loophole" in microzooplankton grazing impact
Univ of Warwick	Genetic diversity, picoplankton and viruses, screening of isolates for activity, climate change impacts on heterotrophic bacteria
Univ of York	Ecosystem functioning, UKPopNET, macroecology

Table 3. Main links between Theme 4 and international research groups and institutions

Genomic approaches for macroalgae (particularly <i>Ectocarpus</i>), phytoplankton diversity and pathogen response	Station Biologique, Roscoff; Banyuls-sur-mer, France, and other partners in EU Marine Genomics network of excellence. Also Alfred Wegener Institute, Germany and Univ of Konstanz
Isolation of stress-related genes	Univ of Galway; IFREMER
Algal-bacteria symbiosis	Univ of Tasmania
Chemical defence potential of diatoms	Max-Planck Institute, Jena
Zooplankton ecology and phylogenetics	Charlottenlund, Denmark; CNRS Roscoff, France; Univ of Patras, Greece; Stazione Zoologica, Naples; Trieste, Italy; Univ of Bergen, Norway; Marine & Coastal Management, Capetown, SA
<i>Calanus</i> ecology and physiology	11 partners & collaborating research groups in Belgium, Croatia, Germany, Italy, Portugal, Spain and Tunisia
Plankton size spectra in the Atlantic; large scale patterns in biodiversity and biogeography	AZTI Spain; Univ of Oslo; Univ of the Western Cape, SA; Univ of Amsterdam
Large-scale long-term patterns, experiments on marine biodiversity and ecosystem functioning, eco-informatics, socio-economics	Partners in EU Marine Biodiversity and Ecosystem Functioning network of excellence (MarBEF; >50 institutes)
Regime shifts; monitoring large-scale long-term change	DFO Nanaimo, Canada; Memorial Univ, Newfoundland; Univ of North Carolina, USA; Florida Fish & Wildlife Research Inst
Scaling the metabolic balance of the oceans	IEO Gijon, Spain
Arctic ecology	Akvaplan-niva, Tromso, Norway
Benthic ecology, mesocosms; bioturbation	NIVA Norway; NIWA, New Zealand
Meiofaunal ecology	Univ of Ghent; Univ of Pernambuco
Fjordic ecosystem ecology	Inst of Oceanology Sopot, Poland
Tsunami effects and recovery, benthic ecology	Kasetsart Univ, Thailand
Habitat selection and behaviour of marine fish	Univ of Bergen; IMC Sardinia
Marine Protected Areas	Univ of Mercia; Univ of Pisa
Intertidal ecology, particularly resource exploitation by intertidal grazers	UCD Dublin; UC Cork; Univ of Goteborg, Sweden; Univ of Lisbon; Univ of Porto, Portugal; Univ of Pisa; Univ of Florence, Italy
Integrated aquaculture	Univ of Bodo; IOLR, Israel
Ecology of artificial reefs and sea defences	IMC Sicily, Univ Bologna; Univ of Goteborg; CEAB Blanes
Statistical methods	Univ of Sydney, Australia; Univ of Auckland, New Zealand; Univ of Bologna, Italy; Univ of Cape Town, SA

Theme-wide stakeholder relevance and Knowledge Transfer activities

All the NERC marine Centres in Theme 4 have obtained, and will continue to obtain, private sector and governmental funding for research that meets specific research-user needs. Such commissioned

research is not presented here; nevertheless, it is the direct consequence of NERC strategic funding. Oceans 2025 will provide the underpinning capabilities, expertise and facilities to continue meeting user needs in future, whilst itself delivering data, information and understanding directed at 'real time' national needs. Major stakeholders were consulted in preparing the proposal, and many components have involved additional discussions with research users. To ensure effective communication between scientists and research users throughout the programme, a Stakeholders Consultation Group will be established for Theme 4 (and other Themes) early in 2007, to meet at 6-9 monthly intervals

Public outreach will continue to be mediated through open days; school liaison and projects; work experience; enhanced web-sites; public lectures; participation in exhibitions, National Science Week events and the annual BA Festival of Science; and active interactions with the media (via press releases, TV and radio interviews).

Theme 4 will inform the 'ecosystem approach' to environmental protection and management as defined in the Convention on Biodiversity and which is at the centre of many national and European marine policy initiatives. Many of those initiatives are closely linked to the development of a UK Marine Bill (to be put before Parliament in autumn 2006) and will contribute to the recently announced EU Marine Strategy Directive.

The science behind implementation of the ecosystem approach, especially with regard to functional processes, is at present poorly developed. The targeted work proposed here will help provide the underlying conceptual basis, also practical advice on management strategies including indicators and monitoring, at spatial scales ranging from ocean basins to individual stretches of coastline. The holistic nature of the ecosystem approach demands attention to the weakest links in the knowledge chain – in particular, the role of microorganisms, genetic diversity, resilience and scales of operation of open ecosystems. Improvements to our knowledge of how marine biodiversity connects with sustainable resource management (linking with Theme 6), marine ecosystem modelling (Theme 9) and wider interactions with the Earth system (Theme 2) will be fed into relevant policy arenas. These outcomes are relevant to all those with an interest in coastal seas and their management, including the EU, Defra, EA, SEERAD, SEPA, EA, EN/NE, CCW, SNH and coastal zone managers. In summary, Theme 4 is an essential component of the UK response to the World Summit on Sustainable Development, with its imperative to halt the decline of marine biodiversity by 2010.

Genetic and molecular approaches will provide new insights and identify potential new goods and services that can be provided by marine biodiversity. Work on biofilms (including cell-to-cell signalling and micro-macro biotic interactions) are important for the understanding and control of biofouling. Bioactive compounds are involved in many interactions between species and will be identified during the course of the work. New genetic markers for algal propagules and larvae will have many applications.

The status of the coastal benthos is regularly monitored by statutory agencies (Cefas and Defra, EN/NE, SNH, EA etc). Quantification of the interactions between benthic and pelagic communities will improve the understanding of the relevance of changes in the benthos to marine ecosystem functioning, within the wider framework of the Defra-led UK Marine Data and Information Partnership (MDIP) and the UK Marine Monitoring and Assessment Strategy.(MMAS).

Elements of the science build on PML's long-term expertise in developing multivariate statistical methods to answer specific scientific questions. We will continue to develop new analyses and to apply them in novel ways (e.g. to bioinformatics data), and where these prove relevant they will be incorporated into the software package PRIMER (developed and marketed by a PML spin-out company; www.primer-e.com). Plankton data from the L4 time series (to be SO 10) are openly available to research users (and the wider public) online (www.pml.ac.uk/L4/) and will be supplemented during Oceans 2025 by historical data on benthos and fish collected by the MBA

stretching back 100 years (e.g. Araújo *et al* 2006 and Theme 10). In addition to the role of BODC (National Facility 1) in data management for Theme 4, sequence and bioinformatics data will be provided to GenBank and other open-access databases. Information on the biology of selected species and biotopes from this research will be made available through *MarLIN* at the MBA (www.marlin.ac.uk) and benthic data archived in the new Defra-funded Data Archive for Seabed Species and Habitats (linking to MDIP and MMAS).

We will share knowledge and data, provide high-level training and collaborate with scientists and environmental economists through our involvement in relevant networks and organisations including MarBEF, EurOceans, Marine Genomics (EU networks of excellence), MetaOceans (EU Marie Curie Action), GLOBEC and advanced training courses.

Strategic Ocean Funding Initiative (SOFI)

Up to 10% of the research science funding for Oceans 2025 will be made available to UK universities and other academic institutions eligible to receive NERC support. Such funding will be awarded for research that is complementary to the Oceans 2025 science Themes, in defined topic areas in a series of funding calls (first call to be announced in 2007). For Theme 4, the following SOFI opportunities have been identified:

- Development of molecular methods
- Testing of novel methods during field programmes
- Widening the scope of mesocosm and field experiments to address additional hypotheses
- Enhancing the geographical spread of the experimental work
- Data sharing and combined analysis to investigate large-scale and long-term issues
- Translating science results into outcomes suitable for incorporation into developing socio-economic and policy-relevant indicators

Summary of Theme-wide outcomes

Theme 4 focuses on elucidating key organisms and processes in the parts of the marine realm thought to be vulnerable to anthropogenic environmental change, but which are missing or poorly represented in current-generation ecosystem models. Working together, we aim to help develop and parameterise new models. The following main outcomes are anticipated:

- Determination of the characteristic scales of variability in coastal and shelf systems to establish baselines against which to measure change
- Quantification of the role of heterotrophic bacteria in primary production
- Identification of the abiotic and biotic factors underlying recruitment and survival mechanisms of key species at the molecular and cellular level.
- Quantitative description of how changes in biodiversity at different levels of biological organisation may impact aspects of ecosystem functioning
- Determination of the relative roles of predators and prey in controlling energy flow through managed coastal ecosystems
- Elucidation of temporally-varying food-web dynamics and links between different ecosystem components, to improve our understanding of non-linear dynamics and processes for new-generation models.

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Acronyms

BODC	British Oceanographic Data Centre	MarBEF	Marine Biodiversity & Ecosystem Functioning
CBD	Convention for Biological Diversity	MDIP	Marine Data & Information Partnership
CCAP	Culture Centre for Algae & Protozoa	MMAS	Marine Monitoring & Assessment Strategy
CCW	Countryside Council for Wales	NF	National Facility (in Oceans 2025)
CFP	Common Fishery Policy	NFSD	NERC Facility for Scientific Diving (at SAMS)
Defra	Department of the Environment, Food & Rural Affairs	NMBL	National Marine Biological Library
DGGE	Denaturing Gradient Gel Electrophoresis	PCR	Polymerase Chain Reaction
DIVERSITAS	International biodiversity programme	PMSU	Prime Minister's Strategy Unit
EA	Environment Agency	RCEP	Royal Commission on Environmental Pollution
EN/NE	English Nature (changing to Natural England)	RFLP	Restriction fragment length polymorphism
ERSEM	European Regional Seas Ecosystem Model	RSE	Royal Society Edinburgh
EU	European Union	SCOPE	Scientific Committee on Problems of the Environment
FAO	Food & Agriculture Organisation	SCOR	Scientific Committee on Ocean Research
FISH	Fluorescence in-situ hybridisation	SEERAD	Scottish Executive Environment & Rural Affairs Department
FRS	Fisheries Research Services (of SEERAD)	SEPA	Scottish Environment Protection Agency
GLOBEC	Global Ocean Ecosystems Dynamics project	SIP	Stable Isotope Probing
HEI	Higher Education Institution	SNH	Scottish Natural Heritage
ICSU	International Council for Science	SO	Sustained Observation (Oceans 2025)
IGBP	International Geosphere-Biosphere Programme	SOFI	Strategic Ocean Finance Initiative
IMBER	Integrated Marine Biogeochemistry and Ecosystem Research	Unesco	United Nations Educational, Scientific & Cultural Organisation
IOC	Intergovernmental Oceanographic Commission	WCO	Western Channel Observatory
IUBS	International Union of Biological Sciences		
IUMS	International Union of Microbial Sciences		